SHORT COMMUNICATION

CARRION FEEDING BY SPIDERLINGS OF THE COB-WEB SPIDER THERIDION EVEXUM (ARANEAE, THERIDIIDAE)

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ABSTRACT. The use of carrient to feed spiderlings has never previously been observed in spiders. Here we show that the theridiid *Theridion evexum* Keyserling 1884 stored dead insectan prey for up to one week prior to the emergence of spiderlings from the egg sac, and continued to feed spiderlings dead prey for six weeks until spiderlings molted to the fourth instar. Spiderlings survived and molted on an experimental diet of exclusively rotten insects.

Keywords: Diet, rotten insects, spiderlings survivorship, prey choice

Generally, spiders are thought to be obligate predators that feed on a wide variety of prey (Bristowe 1958; Foelix 1996). Spiderlings also are predators once they begin to feed (Foelix 1996; GB unpublished data), although the young of some cobweb spiders (Theridiidae) are fed by their mother with freshly caught prey or by regurgitation (Gertsch 1949; Viera et al. 2005). However, numerous examples show that, at least occasionally, spiders in different families feed on carrion (Bristowe 1958; Knost & Rovner 1975; Ross 1981; Pekár 2004), and for some spiders carrion seems to be a primary item in their diet (Sandidge 2003). The use of carrion to feed spiderlings has never previously been observed in spiders, however. Here, we show that mature females of the theridiid Theridion evexum Keyserling 1884 begin to store dead prey several days before spiderlings emerge and that spiderlings can survive and grow on a diet of exclusively rotten prey.

Theridion evexum folds a leaf to form a conical retreat, and makes a small tangle just in front the retreat opening (Barrantes & Weng 2007). Several long threads studded with viscid droplets run from this tangle to other leaves. Prey trapped on these long threads are wrapped and carried into the retreat where the spider feeds. The egg sac is housed within the retreat. After emerging from the egg sac, spiderlings remain in the retreat with their mother until they have gone through three or four molts, at which time they disperse. Large young spiders (5th stage to pre-adult), females without spiderlings, and females with new egg sacs will all discard prey

¹Current address: Department of Entomology, Kansas State University, Manhattan, Kansas 66506 USA. carcasses within a few hours. However, frequently females with spiderlings will accumulate several prey items in their retreats (pers. obs.). Observations on feeding behavior and experiments on prey acceptance of *T. evexum* were made in captivity and in the field, from September 2004 to October 2005, in a 2-ha biological reserve on the campus of the Universidad de Costa Rica, San Pedro, San José Province, Costa Rica (9°54'N, 84°03'W; elev. 1200 m).

To determine whether spiders feed on carrion, we fed them flies in the families Muscidae, Calliphoridae, and Sarcophagidae. Flies were killed by placing them in a freezer for 20 to 30 min (-12° C) and were then immediately placed in a chamber saturated with water vapor at room temperature $(20-22^{\circ} \text{ C})$ for 40– 54 h for field experiments, or 24–63 h for laboratory experiments. After 24 h the muscles of thorax and legs of the decomposing flies had changed from a nearly white tissue to a juicy, red-brownish mass that emanated a pungent "rotten meat" odor. The dead insects were stuck to the vertical viscid threads of the web, which were then vibrated using a tuning fork or forceps. These movements induced the spiders to descend and attack the dead insect.

Mature female spiders in captivity were each placed on a hexagonal truncated-pyramidal wire frame (20 cm high), with a hexagonal cardboard base (7 cm side) to which the spiders anchored their viscid threads (Barrantes & Weng 2007). A paper cone at the apex of the structure served as the spider retreat. The frame hung 2 m above the floor from a thin nylon fishing line.

To test survival and growth on a diet of rotten insects, we formed nine treatment groups by dividing one clutch of each of three females into three groups of spiderlings that were nearly emerged from the egg

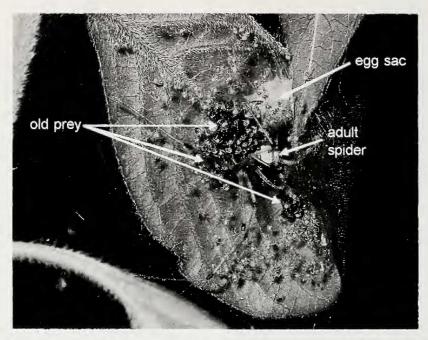


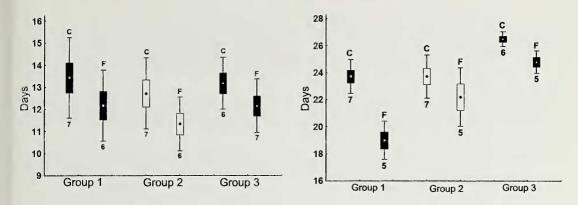
Figure 1.—Mature female of *Theridion evexum* in a retreat that has been opened to reveal the egg sac and the second-instar spiderlings feeding on three dead insects captured two, four, and six days previously.

sac, before they could feed the first time, and placed each group in a separate petri dish (eight groups had seven spiderlings, the other group had six). Spiderlings did not emerge at the same time from the three egg sacs so experiments were not run at the same time for the nine groups. The three treatments were randomly assigned to the groups; thus one group from each clutch was fed rotten insects, the second group, freshly killed insects, and the third group was starved as a control. All insects in this experiment were blow flies (Calliphoridae). Moisture in all petri dishes was provided by a piece of water-soaked cotton. In the rotten-fly treatment, the dead flies rotted at room temperature for 24 h as described previously. Both fresh and rotten flies were pierced four times in the thorax, with an entomological pin, before giving them to the spiderlings. The holes were to facilitate spiderling feeding. Mature females with spiderlings pierced their prey several times, including dead insects, before leaving them for spiderlings to feed upon. We replaced the food for the spiderlings every 24 h and checked for feeding spiderlings three times a day. Instars were counted beginning with emergence from the egg sac (these spiderlings undergo one post-emergent molt inside the egg sac). The intermolt period of the spiderlings to the first and second molts was analyzed using a Randomized Complete Block Design. This analysis of variance allows testing differences among treatments (rotten vs. freshly killed insects) while subtracting the effect of the block (group). Voucher specimens of the

spiders were deposited in the Museo de Zoología, Universidad de Costa Rica.

We additionally fed 23 mature female spiders with decomposing insects in the field. Sixteen of these spiders had spiderlings, and both the adult and the spiderlings fed on rotten insects (Fig. 1). Two spiders with egg sacs wrapped the rotten prey and carried them to the retreat where they hung until spiderlings emerged about four days later. The last five females without egg sacs or spiderlings rejected the rotten insects. In captivity we fed three mature females that had egg sacs, from which spiderlings emerged within 10 days, exclusively with rotten prey. When these spiderlings emerged from the egg sac, they and their mothers were fed exclusively with additional rotten insects until some of the spiderlings reached the third instar. These females accumulated carrion for practically six weeks and spiderlings fed on both very old and newly acquired rotten insects (Fig. 1).

Recently emerged spiderlings fed rotten insects (dead for 24 h) and those fed freshly killed flies molted twice (experiment ended when all spiderlings either molted twice or died). However, the intermolt period to the first molt and to the second molt were shorter for spiderlings fed freshly killed insects (first molt, Fig. 2: F = 7.12, P = 0.01, df = 1, 35; second molt: F = 25.24, P < 0.001, df = 1, 31). Surprisingly, all spiderlings (n = 20) feeding upon carrion survived, but 28% of the spiderlings feeding on freshly dead prey (n = 21) died (*Fisher test* P = 0.03). Mortality occurred in all three groups of spiderlings



Figures 2–3.—Intermolt days to the first (Fig. 2) and second (Fig. 3) molt (mean, standard error and standard deviation) of spiderlings fed carrion (C) and fresh prey (F), from clutches of three different females. Sample size is indicated below each subgroup.

fed with fresh-killed flies. All starved spiderlings (n = 21) died before molting a single time.

The results on growth and mortality of spiderlings indicate that bacteria (or other decomposers) possibly reduced nutrient quality and/or content of prey, as the intermolt period to the first and second molt were longer for spiderlings fed rotten insects. However, it is unclear why fresh-killed prey increased mortality of spiderlings. A possible explanation is that bacteria somehow breaks down some proteins (or other components) that could be indigestible, at least for some spiderlings, thus reducing their mortality. Yet, further investigation is needed to understand how the changes produced by bacteria in the prey reduce spiderlings' mortality.

Spiderlings of other theridiid spiders [e.g. Chrysso cambridgei (Petrunkevitch 1911), Achaearanea tesselata (Keyserling 1884) and Anelosimus studiosus (Hentz 1850)] fed occasionally on dead prey accumulated in their webs for up to one week (pers. obs.). However, T. evexum is the first spider in which carrion feeding plays a central role in rearing offspring since adult females actively save dead prey for their offspring to feed on. At least in T. evexum, C. cambridgei, A.tesselata and A. studiosus the provision of carrion to spiderlings is likely related to the cohabitation of the young spiders with their mother for some time. In these cobweb spiders, spiderlings cohabit with their mother in the same web, at least to the third molt outside of the egg sac (pers. obs.). Saving old dead prey may assure food provision for spiderlings and may be advantageous for maternal spiders as prey is usually unpredictable in time (Wise 1982). It is possible that the use of carrion for adult spiders and as provision for spiderlings may be more frequent when live prey are scarce, as suggested by Knost & Rovner (1975) for wolf spiders.

Spiders of different families have occasionally been observed feeding on dead insects. For instance,

Bristowe (1958) reported Schotophaeus blackwalli (Thorell 1871) (Gnaphosidae) feeding on dead lepidopterans pinned on setting boards. The anteating specialist spider, Zodarion germanicum (C.L. Koch 1837) (Zodariidae), apparently occasionally scavenges on dead ants discarded in the cemetery of ant nests (Pekár 2004). Pholcus phalangiodes (Fuesslin 1775) (Pholcidae), Nephila clavipes (Linnaeus 1767) (Nephilidae) (G. Uhl and W.G. Eberhard pers. comm., respectively) were observed feeding on dead insects hanging for a few days in their webs. Within Theridiidae, three Latrodectus hesperus Chamberlin & Ivie 1935, fed on old dead insects (Ross 1981), and four individuals of Faiditus sp., a kleptoparasite in webs of other spiders (Agnarsson 2003), were observed feeding on their dead spider host (N. clavipes) for more than 16 days (W.G. Eberhard, pers. com.). Knost & Rovner (1975) experimentally demonstrated that wolf spiders (Lycosidae) Schizocosa ocreata (Hentz 1844) as well as Rabidosa rabida (Walckenaer 1837) and Rabidosa punctulata (Hentz 1844) scavenged on old-dead insect parts when freshly killed insects were not available, and Sandidge (2003) described the preference of Loxosceles reclusa Gertsch & Mulaik 1940 (Sicariidae) for dead over live prey. It is also known that matriphagy, where spiderlings sometimes feed for several days on their dead mother, is common in several spiders: Amaurobius sp. (Bristowe 1958) and A. ferox (Walckenaer 1830) (Amaurobiidae) (Kim et al. 2000), Stegodyphus lineatus (Latreille 1817) (Eresidae), and occasionally in A. tesselata (Theridiidae) (pers. obs.). This fragmentary information on scavenging and matriphagy on a wide, phylogeneticaly unrelated range of spiders (Coddington 2005) indicate that, at least occasionally, carrion feeding is widespread among spiders.

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